TURUN YLIOPISTON JULKAISUJA
ANNALES UNIVERSITATIS TURKUENSIS

SARJA - SER. AII OSA - TOM. 259

BIOLOGICA - GEOGRAPHICA - GEOLOGICA

TROPHIC INTERACTIONS OF INVASIVE FOREST HERBIVORES AND CONSEQUENCES FOR THE RESIDENT ECOSYSTEM

by

Tea Ammunét

TURUN YLIOPISTO
UNIVERSITY OF TURKU
Turku 2011

From the Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland

Supervised by Dr. Tero Klemola
Section of Ecology
Department of Biology
University of Turku
FI-20014 Turku
Finland

Prof. Kari Saikkonen
Plant Production Research
MTT Agrifood Research Finland
FI-31600 Jokioinen
Finland

Dr. Kalle Parvinen
Department of Mathematics
University of Turku
FI-20014 Turku
Finland

Reviewed by Prof. Christer Björkman
Department of Ecology
Swedish University of Agricultural Science
SE-750 07 Uppsala
Sweden

Dr. Tarmo Virtanen
Ympäristötieteiden laitos
Helsingin Yliopisto
FI-00014 Helsinki
Finland

Examined by Prof. Matthew P. Ayres
Biological Sciences
Dartmouth College
Hanover, NH 03755
USA

ISBN 978-951-29-4602-0 (PRINT)
ISBN 978-951-29-4603-7 (PDF)
ISSN 0082-6979
Painosalama Oy – Turku, Finland 2011

Muistoissani eläville tukijoille:
Karinille, Mikolle ja Sirkalle

CONTENTS

LIST OF ORIGINAL PAPERS

This thesis is based on the following articles and manuscripts, referred to in the text by their Roman numerals:

I Ammunét T., Kaukoranta T., Saikkonen K., Repo T. & Klemola T.: Invasive and resident defoliators in a changing climate: the egg cold-tolerance of geometrids and predictions concerning outbreak range expansions. *Manuscript.*

II Ammunét T., Klemola T. & Saikkonen K. 2011: Impact of host plant quality on geometrid moth expansion on environmental and local population scales. *Ecography* in press.

III Ammunét T., Heisswolf A., Klemola N. & Klemola T. 2010: Expansion of the winter moth outbreak range: no restrictive effects of competition with the resident autumnal moth. *Ecological Entomology* 35: 45–52.

IV Heisswolf A., Klemola N., Ammunét T. & Klemola T. 2009: Responses of generalist invertebrate predators to pupal densities of autumnal and winter moths under field conditions. *Ecological Entomology* 34: 709–717

V Klemola N., Heisswolf A., Ammunét T., Ruohomäki K. & Klemola T. 2009: Reversed impacts by specialist parasitoids and generalist predators may explain a phase lag in moth cycles: a novel hypothesis and preliminary field tests. *Annales Zoologici Fennici* 46: 380–393.

VI Ammunét T., Klemola T. & Parvinen K.: Apparent competition causing asynchronous population cycles of resident and invasive herbivores. *Manuscript.*

1. INTRODUCTION

What defines the assemblage of species in a community? This is one of the most basic questions in ecology, and one which still puzzles the minds of ecologists. In general, communities have been shaped into their present form by the abiotic environment and by historical and present interactions between organisms. Where abiotic conditions do not limit species existence, interactions with both lower and higher trophic levels have been proposed as the mechanisms that can define the assemblage of existing species (e.g. MacArthur 1958, Hairston et al. 1960, Connell 1961, Price et al. 1980). For insect herbivores, the prevailing hypotheses have fluctuated from the view of Hairston et al. (1960) of higher trophic levels controlling species abundance at lower levels (top-down) to Murdoch's (1966) argument of the greater control of lower trophic levels over the higher ones (bottom-up). More recent conclusions have combined these two views (e.g. Price et al. 1980, Denno et al. 2005, Haukioja 2005).

1.1 Effects of abiotic environment and lower trophic levels on insect herbivores

Especially in northern areas, cold winter temperatures have acted as a barrier restricting species abundance (Bale 1991, Luoto et al. 2006). The cold-tolerance of the dormant insect herbivore for example is affected by both the mechanism regulating the herbivore freezing tolerance and the timing and duration of the cold period (e.g. Bale 1991, 2002, Turnock & Fields 2005). In addition, the cold-tolerance of insect herbivores can change during the overwintering period, thus creating variation in the insect vulnerability to low temperatures during the dormant phase (Nilssen & Tenow 1990, Bale & Hayward 2010).

In addition to temperatures, insect herbivores are naturally affected by the quantity and quality of their host plant (Price et al. 1980, Suomela & Nilson 1994, Virtanen & Neuvonen 1999). The regulating effects of plant quality on insect herbivore communities were first proposed by Murdoch (1966). Food quality, including the host plant response to defoliation, can vary among and within long-lived plants, such as trees (Suomela & Ayres 1994, Suomela & Nilson 1994, Roslin et al. 2006, Stevens et al. 2007). Environmental conditions affect some of the plant traits that define the quality of a plant as food for herbivores (Price et al. 1980). Plant quality as food, however, has also been observed to vary due to different plant genotypes (Horner & Abrahamson 1992, Underwood 2009, Schädler et al. 2010). Variation in host plant quality can shape species distributions. In addition to smaller-scale variation, plant quality as food for herbivores can also vary on a larger spatial scale (Gaston et al. 2004, **II**), and local environmental variation has been suggested to partly define leaf miner abundances (McGeoch & Price 2004).

In addition to varying quality in host plant, interspecific variation also occurs in how good the quality of a given host plant is for the species in question. The host plant

response to defoliation can be species-specific even for closely related herbivore species (DeMoraes et al. 1998). Thus a dominant herbivore can cause the development of plant quality in a particular direction over time (Ahlholm et al. 2002). In forest ecosystems, the long generation time of the host tree imposes limits on how quickly its responses can adjust to a change in selection pressure, for example via cyclic changes in herbivore population densities or via novel defoliators (Smith & Beaulieu 2009). An insect herbivore, with a short generation time, can thus overcome plant responses and quality, which adjust more slowly (Kenis et al. 2009). If the herbivore is able to overcome plant defences, a reciprocal change in host plant responses to defoliation may be launched. A change in the prevailing response to defoliation can in turn mediate indirect effects between herbivore species, if a coexisting herbivore has not adapted to the change in host plant quality (Harrison & Karban 1986, Denno et al. 2000, Anderson et al. 2009).

1.2 Effects of higher trophic levels and competition on insect herbivores

According to Hairston et al. (1960) the world is green because natural enemies keep insect herbivore densities at low levels. While the situation in nature may be more complicated than that, natural enemies can act as a major force in insect herbivore population dynamics. The population dynamics of herbivorous insects regulated by predators and parasitoids generally tend to show an oscillatory pattern (Morris et al. 2005). Furthermore, in the case of many cyclic lepidopterans, specialist parasitoids have been suggested as the driving force of the regular population cycles (e.g. Berryman 1996, Klemola et al. 2010). Specialist natural enemies are capable of driving the population dynamics of their host species due to a delayed, density-dependent numerical response (Turchin 2003). Generalist predators, in contrast, do not usually exhibit a numerical response to prey densities and can thus control herbivore populations only at low densities (Turchin 2003).

Species composition can also be affected by interactions within the same trophic level. Competition is defined as an interaction between two or more organisms, where the interaction is harmful to at least one of the species. Interspecific competition can be direct, through interference, or indirect, via the exploitation of common resources or via shared natural enemies. Apparent competition occurs when the population density of one species is reduced via the numerical response of a shared natural enemy to the increased population density of the other species (Holt 1977).

The dominant competitor may in the long run either outcompete the subordinate one from a location, or the latter may evolve to utilize another resource. Only one of the competing species might thus exist in a given location, as a result of an ecological force, the “ghost of competition past”, (MacArthur 1958, Connell 1983). The same applies to apparent competition via shared natural enemies. The losing competitor may adapt to the competition by moving to an enemy-free space, and the common natural enemy may thus in some localities have only one prey. This “ghost of apparent

competition past" is termed "dynamic monophagy" (Holt & Lawton 1993). Ghost of competition past and dynamic monophagy may prevent the observations of direct and apparent competition (Holt & Lawton 1994).

Interspecific competition has been proposed for various communities as one of the major forces defining their structure by competitive exclusion (e.g. MacArthur 1958, Holt 1977, Chesson 2000, van Veen et al. 2006). With regard specifically to herbivorous insect communities, however, it has been debated whether interspecific competition may be a possible agent in defining species composition (Hairston et al. et al. 1960, Connell 1983, Denno et al. 1995). Evidence of both direct and indirect competition as factors shaping insect herbivore communities has nevertheless been accumulating (Denno et al. 2000, Redman & Schriber 2000, Kaplan & Denno 2007, Preisser & Elkington 2008).

The tendency of herbivore populations to cycle often makes it more difficult to observe apparent competition (Morris et al. 1995). In general, cyclic dynamics are thought to often dampen the effects of apparent competition (Abrams et al. 1998). A shared parasitoid, for example, can nevertheless have a zero, negative or positive effect on the host species, with population dynamics varying from cycles to stability or even the extinction of one of the species (Brassil & Abrams 2004). When competition between the herbivores is included, the outcome of apparent competition can be very diverse in different communities (Holt & Lawton 1994). Generalist predators, for example, can dampen the cycles in prey populations, and may promote the coexistence of competing species when the dominant competitor is more affected by predation (Chase et al. 2002).

1.3 Invasive species and resident community

The recent radical changes in the global climate have brought basic questions of species abundances and community structure to the table once more, as changes in temperature have either driven species to the verge of extinction or have allowed them to expand their ranges into new areas (McLaughlin et al. 2002, Parmesan 2006, Walther et al. 2009). Recently invaded ecosystems and ongoing invasions create an arena for "natural experiments", where interactions between lower and higher trophic levels can be observed before they are obscured by effect of adaptation (Sakai et al. 2001, Holt 2009).

Global warming is predicted to raise boreal winter temperatures in particular. Overall, the boreal zone is expected to experience a temperature rise of 3.5–5˚C during the next 90 years (Lindner et al. 2008). In addition, current climate-change scenarios predict a radical increase in the probability of precipitation, especially during the winter season (Lindner et al. 2008). Recent studies have indeed shown the spreading of many species to areas where the cold climate was formerly a limiting factor (Parmesan et al. 1999,

Bale et al. 2002). In particular, many lepidopteran species, including forest pest species, have moved into more northern latitudes (Hickling et al. 2006, Jepsen et al. 2008).

New species spreading into an area, termed invasive species (e.g. Colautti & MacIsaac 2004, Lockwood et al. 2007), are in general characterized by certain life history traits (Lodge 1993, Kolar & Lodge 2001). For example a high rate of population increase, good competitive ability and tolerance/adaptation to a broad range of environmental conditions enable the establishment of a viable founder population and help the species spread further (Sakai et al. 2001, Delatte et al. 2009). These features are often merely enhanced by the warming climate (Berggren et al. 2009, Walther et al. 2009). A new species may on the other hand be prevented from spreading in the new area by unfavourable abiotic conditions, lack of suitable resources, competitive exclusion by the resident species, or predation (Holt & Lawton 1994, Chesson 2000, Kaplan & Denno 2007, Berggren et al. 2009). If an invader successfully spreads to a new area, the existing links and interactions among the resident (indigenous) organisms in the community are at risk to be radically changed. The effects of invasive species range from altering the genetic composition of local populations and species to trophic cascades affecting all trophic levels in the community (Sakai et al. 2001, Tylianakis et al. 2008, Kenis et al. 2009). Assessment of the potential threat to a given ecosystem calls for a comparison of the life-history characteristics of the resident and invasive species (Sakai et al. 2001).

Genetic diversity, especially in traits affecting fecundity, creates the potential for an invasive species to adapt to novel environments and native species (Sakai et al. 2001, Lee 2002; but see Tsutsui et al. 2000). The response to the selection pressure generated by the novel environment may contribute to creating larger genetic variance and hence successful adaptation by the invading species (Sakai et al. 2001). Invading species can thus be extremely effective in adapting to the variability of environmental conditions and for example to the host plant quality encountered (e.g. Mooney & Cleland 2001, Walther et al. 2009). Good adaptation capability to new conditions can launch rapid evolutionary changes in both resident and invasive species via genetic drift and natural selection (Sakai et al. 2001, Strauss & Irwin 2004). For example, if adaptation to host plant quality creates a selection pressure diverging significantly from that due to resident species, permanent changes in host plant quality may be seen on an evolutionary scale (Lambrinos 2004, Strauss et al. 2006, Wise 2009). This altered host plant quality may then drive further changes in the resident species and in the whole ecosystem (Strauss et al. 2006, Lau 2008).

In addition, invasive species can create new links in the local community by competing directly and indirectly with native species. Shared resources, spatiotemporal co-occurrence and ecological similarity may all strengthen competitive interactions between two species (Schoener 1974). Competition with a closely related resident species in particular can thus induce changes in the community. Invasive herbivores,

for instance, can outcompete native species and exclude them from the local community (reviewed in Kenis et al. 2009). However, interspecific competition between herbivores can also have positive consequences for a host plant by suppressing the densities of the more harmful defoliator (Preisser & Elkington 2008). Invasive herbivores can also affect the resident herbivore population by apparent competition via shared natural enemies (Redman & Schriber 2000). A rapidly advancing invasive species, with a short life cycle, can easily escape specialist natural enemies belonging to the original species range (e.g. Menéndez et al. 2008). The invader may thus encounter lower mortality from predation. In addition, the invasive species may favour an increase in the generalist predator community, thus increasing predation pressure on resident competitors. Thus the invader can affect the local community on several levels (Jones et al 1998).

1.4 Geometrid moths in northern Fennoscandia

Forest ecosystems in northern latitudes can be particularly vulnerable to effects induced by new invasive species, since they are generally characterised by simple food webs, slow biological processes and low species numbers (e.g. Sakai et al. 2001). Fennoscandian boreal and especially sub-arctic forests are representative examples of such simple ecosystems.

The Finnish part of northern Fennoscandia was previously dominated by the autumnal moth (*Epirrita autumnata* [Borkhausen] [Lepidoptera: Geometridae]) which feeds mainly on the leaves of the mountain birch (*Betula pubescens* ssp. *czerepanovii* [Orlova] Hämet-Ahti [Fagales: Betulaceae]). The population cycles of this species are well known (Tenow 1972, Lehtonen 1987, Haukioja et al. 1988, Klemola et al. 2002), and recent evidence shows that parasitoids may be the driving agent causing them (Klemola et al. 2008, 2010). In extreme cases, the peak population-cycle phase of this outbreaking species can transform vast areas of mountain birches from verdant forest into treeless tundra (Tenow 1972, Lehtonen & Heikkinen 1995).

During recent years another cyclic moth defoliator, the winter moth (*Operophtera brumata* Linnaeus [Lepidoptera: Geometridae]), has also extended its outbreak range to these mountain birch forests (Hagen et al. 2007, Jepsen et al. 2008, 2009, Klemola et al. 2008). Taking advantage of the rising winter temperatures, the winter moth has spread from the more temperate Norwegian coasts in the north (kept warm by the Gulf Stream) to the colder continental areas in Finnish Lapland (Bylund 1999, Jepsen et al. 2008, **I**). The winter moth was previously considered a threat only in western and central Europe (Lindner et al. 2008); now, however, it has already caused severe defoliation to mountain birch forests in its new outbreak range (Klemola et al. 2008, Jepsen et al. 2009).

The two moth species are highly similar in their life-cycle (for details see 2.2). The resident autumnal moth and the invasive winter moth are both attacked by shared

generalist predators and parasitoids that lack other host alternatives in these areas (Ruohomäki et al. 2000, Klemola et al. 2002, **V**). Where the two species have previously been known to coexist in the north, for example on certain mountain slopes, they tend to prefer different altitudinal zones: autumnal moths are most abundant at the medium and high altitudes, and winter moths at low and medium altitudes (Tenow 1996, Mjaaseth et al. 2005). As a consequence of these similarities, autumnal and winter moths are bound to interact, directly and indirectly, at all stages of their univoltine life-cycle.

Where their outbreak areas overlap, the population dynamics of the two insect herbivores have often been observed to be phase-locked, but with the cycle phases of the winter moth lagging 1–3 years behind those of the autumnal moth (Tenow 1972, Hogstad 2005, Tenow et al. 2007). These asynchronous population cycles have also been observed in the new sympatric area, creating almost continuous high defoliation pressure on the shared host plant (Klemola et al. 2008, **V**); food quality is thus ruled out as the reason for this asynchronicity in population cycles. Apparent competition via shared predators and parasitoids has been suggested as an explanation for the phase-lagged cycles of the winter moth (Klemola et al. 2008, **V**). A strong preference (or full specialization) by a shared natural enemy for one of the two moth species could suppress the densities of the preferred moth species and allow those of the other species to increase.

In addition to the winter moth, yet another geometrid moth species now threatens to invade the mountain-birch forests of northern Fennoscandia. The scarce umber moth (*Agriopis aurantiaria* [Hübner] [Lepidoptera: Geometridae]) has a life history very similar to the autumnal and winter moth and has reached outbreak densities with the potential for large-scale defoliation. During recent years the scarce umber moth has spread north through coastal northern Norway (Nilssen 2007, Jepsen et al. 2011), closely resembling the range expansion route of the winter moth (Jepsen et al. 2008).

1.5 Aims of the thesis

The invasive winter moth has a significant potential to expand its outbreak range even further inland and affect the mountain birch community by direct and indirect interactions. In addition, a strong potential may exist in the scarce umber moth and to a lesser extent in another two potential invaders to spread their ranges towards the mountain-birch forests in northern Finland (see **I**). The aims of this thesis were to investigate the potential in these species to spread to new areas in the north and to find out in what extent the new species may affect the resident species and the whole mountain birch ecosystem via interactions. To answer these main questions, I have investigated possible factors affecting these new invaders: I have also looked in greater detail at interactions between the winter moth and the mountain birch ecosystem in northern Finland. I have explored the effects and interactions at multiple trophic levels: from the effects of restrictive abiotic conditions to host plant quality and interspecific

interactions, including indirect interactions and trophic cascades potentially induced by the invasive species. In the individual case studies I have used various methods, from laboratory tests to experiments in nature, investigating factors ranging from genetic diversity to larger regional units and from a relatively short time span to evolutionary hypotheses.

In case study **I** I studied the cold-tolerance of the winter moth and other potential invasive geometrids in the laboratory, measuring the ice nucleation temperatures of overwintering eggs. I also tested overwintering survival in relation to minimum winter temperatures in an experiment in natural conditions and compared the cold-tolerances of the invaders to that of the resident autumnal moth. Based on the cold-tolerance results and on published models of the effect of global warming on winter temperatures in boreal Fennoscandia, I predicted the extent of possible further expansion of the outbreak range and the possibility of other potential invaders shifting their ranges to these areas.

In study **II** I explored the responses of the rapidly expanding winter moth and the potentially invasive scarce umber moth to host-plant genetic and local environmental variation, in order to determine the adaptation potential of these invasive pests. The invaders were compared to the resident autumnal moth in order to discover the spreading potential of the invasive species. Larval performances were recorded on eleven genetically diverse mountain birch families originating from central Lapland and from the Utsjoki area. Rearing took place in two different environments in order to determine the effect of variation in local environmental scale in addition to effects occurring on a larger geographical scale and in relation to host plant genotype. Adaptation potential was investigated by measuring variation in moth fecundity due to host genotype. Finally, I investigated whether the quality of the host tree is the same for all three species, and whether selection pressure from the defoliators directs the population genetic structure of host tree resistance in the same or the opposite direction. This was done by comparing the genetic and phenotypic correlations of mountain birch quality between the invaders and the resident moth species.

Direct and indirect interactions between the invasive winter moth and the resident autumnal moth were investigated in studies **III**, **IV** and **V**. Direct interference/exploitation competition and indirect host-plant–mediated apparent competition were studied in two field experiments (**III**). To uncover direct competition, the performance of moths reared in mixed-species mesh bags at different densities was compared to that of the same species reared in single-species mesh bags. Similarly, moth performance after rearing in mixed-species trees was compared to moths reared in single-species trees in order to determine possible apparent competition via changes in host plant quality. Short-term apparent competition via generalist pupal predators and larval parasitoids was similarly examined by comparing predation and parasitism rates in a mixed-species and a single-species experimental setup (**V**). In addition, the

functional response of generalist pupal predators and predator preference for autumnal and winter moths were investigated in a mixed-species setting at equal and varying densities (**IV**, **V**). Finally, parasitoid preference for the invasive and the resident species was investigated by comparing parasitoid assemblage and parasitism rates in an experimental setup and in field-collected larvae (**V**).

The causes underlying the puzzling asynchrony of the autumnal and winter moth populations were hypothesized and investigated in studies **III**, **IV**, **V** and **VI**. With high densities at the peak phase of the cycle, strong asymmetric interspecific exploitation competition could act to start a decline in the population density of the subordinate competitor (**III**). A strong parasitoid preference for one species could also set off an earlier start of the decline phase, while letting the densities of the less preferred species rise up to a certain threshold (Klemola et al. 2008, **V**). The bottom and increase phases of the cycle could be affected by generalist predator preferences or diverse functional responses with respect to the two species (**IV**). The findings from the short-term experiments were utilized in study **VI**, where the probability of parasitoid preference and other asymmetric events in contributing to the observed asynchrony were modelled. A Nicholson-Bailey type model was used as the starting point, in which the invasion of the winter moth was added using the adaptive dynamics theory. Long-term effects of asymmetric competition were investigated in parameter space defining the strength of parasitism preference and the asymmetric effects of generalist predation. The future of asynchronous population dynamics, and of moth population dynamics in general, are also discussed in the article.

2. MATERIAL AND METHODS

2.1 Study area

The study areas were located in the continental boreal and sub-arctic areas of Fennoscandia. The landscape is dominated by mountain birches as the most common tree species in these areas (Wielgolaski 1972). The average winter temperature is -13˚C, but extreme temperatures of -40˚C and below occur quite often (Turnock & Fields 2005). Milder winters are usually encountered in the more coastal areas of the sub-arctic zone. The average temperature sum over the year, on a basis of +5˚C, does not normally exceed 700 (Luoto et al. 2006), meaning that the growing season is relatively short.

Studies **II**, **III** and **IV** in their entirety and studies **I** and **V** for the most part were carried out in the vicinity of the Kevo Subarctic Research Station (69°45'N, 27°01'E, Figure 1A) in northernmost Finnish Lapland (Utsjoki municipality). One study site was established closer to the coastal boreal areas in Nuorgam (70°04'N, 27°52'E, study **I**), 48 km from the research station.

Two tree-line gardens (TLG1 and TLG2) were established close to the Kevo Subarctic Research Station in the 1970s (Kallio et al. 1986). Seeds from individual trees (such as mountain birches) were collected from all over northern Fennoscandia, and the free-pollinated progenies of the mother plants (half-sib families) were planted in the gardens. These gardens were used for the experimental setup in study **II**.

Two study sites in northern Norway were also used in the experiments. Of these, Skippagurra (70°09'N, 28°13'E) is located approximately 65 km north east of Kevo and was used in the experiment in study **V**. The Hana (70°14'N, 28°27'E) study site was used in studies **V** and for the observational data for study **VI**. This most distant study site is located approximately 80 km from the Kevo Research Station.

2.2 Study species

2.2.1 Autumnal moth and winter moth

Autumnal moths and winter moths are univoltine forest-dwelling defoliators that use the mountain birch as their main host in northern Fennoscandia. The eggs hatch simultaneously with the mountain birch bud break, and the larvae feed on the leaves throughout the five instars. Winter moths feed inside a leaf roll with the leaves wound loosely together while autumnal moth larvae feed freely on the leaf (Figure 1B and C). After the larval period, the moths pupate in the ground. Autumnal moth adults eclose from mid-August onwards, with winter moths following autumnal moths by a few weeks, and the females lay their eggs on tree trunks and branches. Autumnal moth females are relatively poor flyers, and the wingless winter moth females are totally flightless. Pupal weight correlates strongly with the realised fecundity of the adult

female in both species (Haukioja & Neuvonen 1985, Tammaru et al. 1996, Heisswolf et al. 2009, **V**). The moth eggs overwinter, with a slight difference in temperature tolerance: autumnal moth eggs can survive temperatures as low as -36˚C (Nilssen & Tenow 1990, Virtanen et al. 1998, **I**), while winter moth eggs usually die at approximately -35˚C (MacPhee 1967, **I**).

The two moth species share their generalist invertebrate and vertebrate predators. These include for example ants, beetles, spiders, birds and small mammals (e.g. voles and shrews), that attack the moth eggs, larvae and pupae. In addition, autumnal and winter moths are attacked in all life stages by parasitoids. A parasitoid is an insect or other organism which spends a significant portion of its life cycle attached to or within a single host organism which it ultimately kills in the process. Some parasitoids are shared by the autumnal and the invasive winter moth (**V**).

Both moths exhibit population cycles with a period of nine to eleven years (Tenow 1972, Bylund 1999, Klemola et al. 2002). Overall the cyclic densities may vary from almost none to nearly 1000 larvae per 1000 short shoots or even higher (Haukioja et al. 1988). The peak population densities sometimes reach outbreak status, and this may cause severe large-scale defoliation of mountain birches and even tree deaths (Tenow 1972, Lehtonen 1987, Haukioja et al. 1988, Lehtonen & Heikkinen 1995, Klemola et al. 2007, 2008, Jepsen et al. 2008, 2009).

2.2.2 Potential invaders

In addition to the winter moth, other moth species, with similar life history characteristics, have the potential to invade mountain birch forests in northern Finland. The larvae of the scarce umber moth also feed on mountain birch leaves; their larval colour, however, resembles birch branches, unlike the colour of autumnal and winter moth larvae (Figure 1D). Scarce umber moths pupate at approximately the same time as autumnal and winter moths, but the adults eclose slightly later than winter moths. Like winter moth females, scarce umber moth females are wingless and totally flightless. In Finland, the species range of the scarce umber moth is restricted to southern areas (Figure 1A). Two other geometrids, the mottled umber moth [*Erannis defoliaria* (Clerck)] and the northern winter moth [*Operophtera fagata* (Scharfenberg)], are also found in more southern parts of the country than the autumnal or winter moth (Figure 1A). In their present range, the larvae of these species feed on birches or mountain birches. The adults eclose late in the autumn; the females of these two southern species are again wingless. One novel study on the species range advancement of the scarce umber moth can be found (Jepsen et al. 2011), but no previous studies on the invasion potential of the two southern species or on the performance in mountain birch forests of any of the three species have to my knowledge been published.

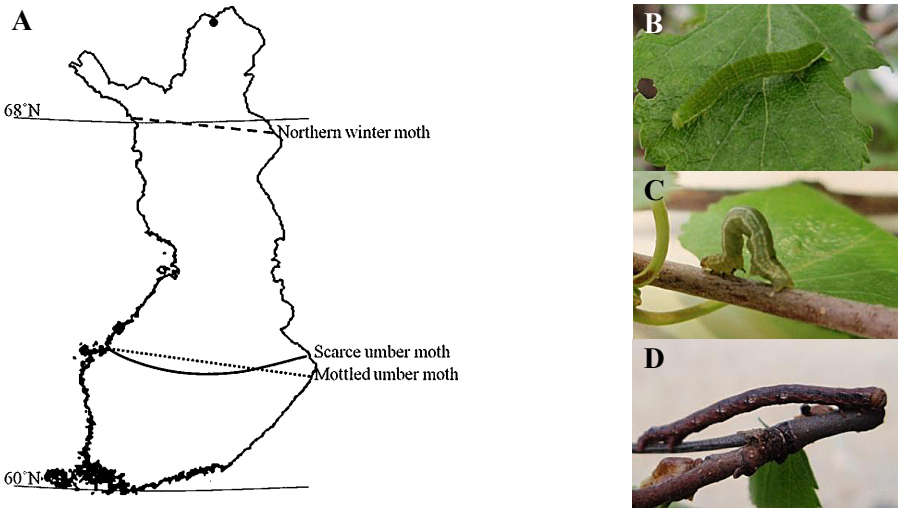

Figure 1. Study area and species. A: Map of Finland and the Kevo Subarctic Research Station (filled circle). The approximate northern limit of the species ranges for scarce umber, mottled umber and northern winter moth in Finland are shown by various lines. Larvae of the autumnal (B), winter (C) and scarce umber moth (D) are shown in photographs.

2.3 Experimental procedures

In the following, I outline the methods used in the original articles and manuscripts. The methods used, and the statistical and mathematical analyses, are described in more detail in the respective articles and manuscripts.

2.3.1 Experimental larvae, pupae and eggs

Experimental larvae were chosen randomly for the experiments from a large set of lab-reared (**II**, **III**, **V**) or field-collected (**III**, **V**) larvae. Young, second or third instar, larvae were released to feed on mountain birch leaves either in parasitoid proof mesh bags (**I**, **III**) or freely in natural conditions (**V**). The larvae used in the mesh bag experiments were reared in the experimental settings throughout their larval period and collected from the field in their prepupal stage. Prepupae were allowed to pupate in individual vials in *Sphagnum* moss.

Ten-day-old pupae were sexed and weighed for fecundity measurements and for the pupal experiments (**IV**, **V**). In the pupal experiments the pupae were buried in soil or moss either inside small plastic cages or with their pupal cocoon visibility enhanced by glitter (for the latter method see Tanhuanpää et al. 1999). Each pupa buried in the cages was marked individually. The locations of the buried glittering pupae were marked with a wooden stick, but no individual weight or sex information was maintained. After two to five weeks exposure, the pupae were re-collected and their fate was checked for invertebrate and vertebrate predation and parasitism.

Twenty females from northern populations of autumnal and winter moths and fourteen scarce umber females were mated with random males and allowed to lay eggs. Southern autumnal moths were collected as larvae from Naantali and Vahto in the vicinity of Turku, while southern samples of winter, scarce umber, mottled umber and northern winter moths were collected as adults from the Botanical Garden of the University of Turku (60˚26' N, 22˚10' E), located on the island of Ruissalo in southwest Finland. Eggs from the progenies of nine each of autumnal, winter and scarce umber moth, five mottled umber moths and two northern winter moths from the southern populations were used in the experiments concerning egg cold-tolerance (Figure 2, **I**).

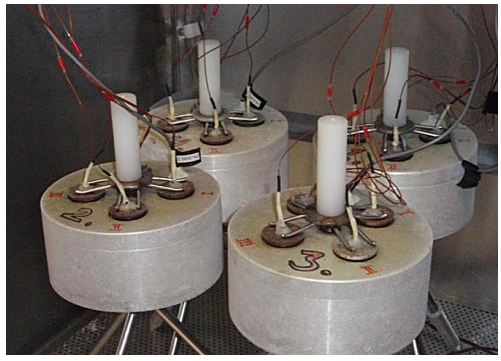

Figure 2. Setup for the cold-tolerance laboratory test. Eggs of five moth species were used to compare egg cold-tolerance between invasive, potentially invasive and resident moth species in a laboratory test. Egg cold-tolerance was measured in a chamber with four units. Each unit consisted of one control tube and three test tubes. Temperature differences between the control and test tubes were measured while the ambient temperature in the chamber was gradually lowered to -50˚C.

2.3.2 Egg cold-tolerance

The egg cold-tolerances of northern and southern moth populations were tested in the laboratory by determining the ice nucleation temperature (**I**). This was done by means of differential thermal analyses (DTA, Veteli et al. 2005): the differences in temperature between an empty control tube and the three test tubes with the eggs were recorded while the ambient temperature was reduced by 5˚C per hour down to -50˚C (Figure 2). A sudden peak in the thermal difference indicates the ice nucleation, i.e. the death, of an egg (Figure 1 in study **I**). The median peaks from the DTA analyses were compared among species and populations in order to determine the differences in the potential for cold-tolerance.

The cold-tolerance of moth eggs in natural conditions was examined by establishing three altitudinal transects (**I**): two located near the Kevo Subarctic Research Station and one in Nuorgam. The altitudinal transects were used to obtain a naturally varying minimum temperature range at the overwintering sites. Eggs from the northern moth

populations were placed at five points along the transects, either on natural material (autumnal and winter moth) or in small, closed plastic tubes (scarce umber moth). Data loggers recorded minimum temperatures at each transect point. The eggs were allowed to overwinter from October through May, when they were re-collected and their state was checked in the laboratory (Figure 3). The survival probabilities of the moth eggs were compared among species, transects and minimum temperatures at transect points.

Figure 3. Examples of moth eggs under inspection with a microscope. The state of each moth egg was checked with a microscope after overwintering at one of the three transects. Left: fertilised, red, autumnal moth egg laid on a twig. Centre: dead moth egg after overwintering. Right: empty moth egg (larva already hatched).

2.3.3 Maps of minimum daily temperatures

Temperature maps of past and future winter minimum temperatures were drawn according to observed species-specific cold-tolerances for the autumnal, winter and scarce umber moth (**I**). These cold-tolerances were used as threshold values, in calculating the frequency of years with minimum temperatures below or at the threshold value. Maps were drawn both for past minimum temperatures for the years 1950–2009 and for predicted minimum temperatures for 2011–2040 (Figure 4 and S2 in study **I**). Predicted values were based on the median of minimum temperature predictions from seven Global Climate Model (GCM) and Regional Climate Model (RCM) pairs obtained from published data. The resulting maps served as a basis for predicting the expansion of the invasive winter moth and the potentially invasive scarce umber moth.

2.3.4 Variation in food quality

Variation in experienced food quality due to host plant genotype and location was investigated in study **II**. Autumnal and winter moth larvae were reared in mesh bags on 11 half-sib mountain birch families. Four of the 11 half-sib families originated from central Finnish Lapland (C), the other seven from the Utsjoki area (U). Two mesh bags, each containing 11 larvae of either the autumnal or the winter moth, were placed on four trees from each half-sib family (Figure 4). The experiment was carried out in both tree-line gardens (TLG1 and TLG2). In TLG1 a third mesh bag, containing nine scarce umber moth larvae, was placed on two trees from nine families. Due to the small number of scarce umber moth larvae, this was not repeated in TLG2.

Differences in resident and invasive moth life history parameters were investigated according to tree family, small scale environment (TLG1 or TLG2) and larger scale environment (C or U). In addition, I estimated variation in pupal mass and fecundity according to tree genotype. Genetic variance (V_A) and the coefficient of genetic variation (CV_A) were calculated from the observed variances according to Houle (1992), Falconer & Mackay (1996) and Fry (2004). Furthermore, genotypic and phenotypic correlations were used to investigate possible cascading effects via selection pressure changes in plant responses due to invasive species (Ahlholm et al. 2002).

Figure 4. General setup for mesh bag rearing. This experimental setup was also used in the tree-line garden experiments for measuring the effects of food quality on moth larvae. Most of the trees held two mesh bags, with one bag containing autumnal and one winter moth larvae. A few trees also held a third mesh bag, containing scarce umber moth larvae.

2.3.5 Competition experiments

Direct interspecific competition and the strength of intraspecific competition were explored in study **III**. To study direct competition, autumnal (AM) and winter moth (WM) larvae were reared in a set-up with both species (mixed-treatment) or only one species (single-treatment) present in the mesh bag, in three densities (total 10, 20 or 30 larvae per mesh bag; Figure S1 B in study **III**). All three treatments were placed on one polycormic tree. Each density was repeated on eight individual mountain birches, the overall number of density replicates thus being 24. The pupal masses of larvae reared in the mixed-treatment were then compared to those in the single-treatment.

In study **III**, indirect competition via host plant was also explored. Ten groups of three trees each were selected for the experimental setup (Figure S1 A in study **III**). Each tree held two mesh bags (as in Figure 4), each with 20 larvae from one of the two species. The trees were divided into single- or mixed-treatment. In the single-treatment

trees, larvae of only one species – autumnal moth (AM) or winter moth (WM) – were feeding on the tree. In the mixed-treatment tree, one mesh bag held larvae of the autumnal moth, and the other those of the winter moth. The pupal masses of larvae reared on mixed-treatment trees were compared to those reared on the corresponding single-treatment trees. Differences in pupal masses between mixed-treatment and single-treatment trees would reflect the effect of changes in food quality for one species in the presence of the other.

Differences in pupal predation between autumnal and winter moths, and the functional response of invertebrate and vertebrate pupal predators, were investigated in studies **IV** and **V**. In study **IV**, pupae were buried in the soil in small plastic cages at two transects. Each transect held ten study patches with seven different pupal densities (2, 3, 4.5, 8, 12.5, 18 or 36 pupae/m^2, Figure 1 in study **IV**). The three lowest densities were each repeated twice per transect. Each buried cage held one autumnal and one winter moth pupa, except at the highest density, where two pupae per species were placed in one cage. In study **V,** ten pupae with glittering cocoons were buried at four parallel transects. At each transect, pupae from only a single species were buried in the soil. Three transects were chosen for autumnal moth pupae and one for winter moth pupae. The set of four transects was repeated at five locations.

Indirect short-term apparent competition via natural enemies was studied in article **V**. Larval parasitism was studied by collecting samples of both species from a sympatric area at Hana and in an experimental study in the Kevo area (**V**). In the experimental study, autumnal and winter moth larvae were grown on trees on five study plots. The setting was similar to that used in study **III**: each study plot consisted of four single-treatment trees with autumnal moths, four single-treatment trees with winter moth and four mixed-treatment trees with both species (Figure 2A in study **V**). The four trees chosen to represent the same treatment were close to each other, while the distance between treatments was approximately 40 meters. 40 larvae per tree were first grown in mesh bags and then allowed to feed freely on the foliage for eight days; they were then re-collected and reared through the remaining instars in the laboratory. Parasitism was checked from later larval instars and pupae. Short-term apparent competition via pupal predators was investigated by burying pupae in the soil in cages. Cages were buried at two study sites and one transect. Four patches were established in a diamond shape: single-treatment with autumnal moth, single-treatment with winter moth, and two mixed-treatment patches (Figure 2B in study **V**). In addition, three transects were established at Skippagurra with mixed-treatment cages only. Parasitism and predation probabilities were compared between the mixed- and single-treatments of each individual species and between species.

2.3.6 Modelling

In study **VI,** I used a mathematical model to explore the possible outcomes of the invasion of winter moths into the mountain birch ecosystem. More specifically, I

investigated the impact of observed short-term asymmetric effects via generalist predators and parasitoids on the long-term population dynamics of the winter and autumnal moth. In addition, I examined the possibility of apparent competition as the cause of the time lag between the population cycles of the autumnal and winter moth in the sympatric area at Hana. A Nicholson-Bailey type model was constructed to describe the dynamics of two moth species sharing a solitary late larval parasitoid and suffering from the asymmetric effects of competition via a generalist predator (Equations 1 and 2 in study **VI**). The model dynamics were first studied with the presence of one moth species and the parasitoid. In the second stage an invasion of the second moth species was added and the possibility of coexistence of two moth species and evolutionary consequences of the invasion were investigated using the framework of adaptive dynamics theory.

The fate of the invader population, according to the invasion fitnesses calculated for mutations in trait m (parasitism probability and asymmetric effects of competition) was studied in an environment created by the resident population. The signs of invasion fitnesses in dependence on resident and mutant strategies (trait values) were plotted. A range of pairs of trait values, when the coexistence of the two populations is possible, was then defined according to positive invasion fitness for both populations. The natures of the singular strategies, representing the possible endpoints of evolution in the three-species system, were studied from the pairwise invasibility plot thus formed. Possible evolutionary outcomes and population dynamics following the invasion were examined. Finally, the long-term effects of apparent competition were investigated by comparing the average population density of the resident species in one-moth environment to the average population density after invasion by the second moth species.

3. RESULTS AND DISCUSSION

3.1 Survival of moth eggs in a changing climate

As also previously reported (MacPhee 1967, Nilssen & Tenow 1990), cold-tolerance differed between autumnal and winter moths by approximately one degree (˚C) measured with DTA (Figure 3 in study **I**, Table 1). A small difference was also observed between northern and southern populations, with the southern populations of all species studied tolerating slightly lower temperatures (**I**). More notably, scarce umber moth eggs required temperatures several degrees higher than autumnal or winter moths for survival; they are thus not likely in the near future to spread to areas with a continental climate. The cold-tolerances of mottled umber and northern winter moths from southern populations were higher than those found for the scarce umber moth, but lower than those of the winter moth. While the results for the two southern species might be only indicative, the cold-tolerance results suggest a potential also in these two species to spread to more northern areas.

Table 1. Cold-tolerance results for all five moth species. Cold-tolerances were investigated for all five study species in a laboratory test. Means of the median ice nucleation temperatures are shown with the corresponding 95 % confidence limits obtained from the statistical analyses (described in more detail in study **I**). Results shown by species and by population origin.

	South population		**North population**	
Species	*Mean (˚C)*	*95 % cl*	*Mean (˚C)*	*95 % cl*
Autumnal moth	-37.0	±0.5	-36.7	±0.6
Winter moth	-36.5	±0.5	-35.8	±0.5
Scarce umber moth	-31.5	±0.5	-31.2	±0.5
Mottled umber moth	-33.4	±2.7		
Northern winter moth	-35.6	±2.4		

The naturally variable winter conditions reduced survival probability already at temperatures a couple of degrees higher than the cold-tolerances measured with DTA (**I**). This difference was probably due to differences in the dormant stage of the moth eggs between the laboratory and the field tests (Nilssen & Tenow 1990, Virtanen et al. 1998). Cold-tolerances in natural conditions at two transects nevertheless reflected overall differences between species. Autumnal moths tolerated cold temperatures slightly better than winter moths, but the overall response to falling temperatures was the same for both species (Figures 2A and 2B in study **I**). At the third transect, other abiotic conditions than temperature, such as humidity or wind conditions, probably had

a negative effect on overwintering autumnal moth eggs, but little or no effect on winter moth eggs (Figure 2C in study **I**). This suggests that such abiotic conditions might play a greater role in insect cold-tolerance than previously thought. In the case of the scarce umber moth eggs, the minimum winter temperatures at the study sites were lower than the median cold-tolerance found for this species; thus none of the eggs survived the winter of the study year.

The minimum winter temperatures in continental boreal and sub-arctic areas have become milder over the last decades (Figure S2 in study **I**). This has allowed the expansion of the winter moth outbreak area. The temperatures, however, are not high enough to allow the scarce umber moth to spread to continental areas (Figure S2 in study **I**). According to global warming predictions, lethal winter temperatures for autumnal and winter moth eggs will only rarely be reached over the next 30 years (Figure 4 column C in study **I**). Areas, with winter temperatures lethal for the scarce umber moth are also predicted to diminish (Figure 4 column C in study **I**). In the future, the species ranges of all three geometrid moths may thus expand.

3.2 Adaptation to host plant quality variation

Study **II** investigated and compared adaptation to food quality variation, on a genetic, environmental and geographical scale, in the resident autumnal moth, the invasive winter moth and the potentially invasive scarce umber moth. Pupal masses of the invasive winter moth were less strongly affected by the variation in host plant quality than were those of the resident autumnal moth (Figure 1 in study **II**). Tree family, environment and geographical origin of the tree family all gave rise to more variation in autumnal moth fecundity than in that of the winter moth. The effects of natural variation in mountain birch quality have previously been shown to affect moth fecundity (Hanhimäki et al. 1994, Virtanen & Neuvonen 1999). The results for the winter moth and the scarce umber moth indicate that significant differences may occur in the effect of host plant quality, even in closely related invasive species.

The development time of winter moth larvae, however, varied greatly due to tree family, environment and geographical origin of the tree family (Figure 2 in study **II**). In the case of the autumnal moth environmental and geographical origin were less important as causes of variation in development times. In general, it is known that insect defoliators are able to compensate at least to some extent for poor host plant quality with longer development times (Ayres & Maclean 1987, Roslin & Salminen 2009). Thus the winter moth may be relatively good at compensating for poor food quality: winter moths showed a relatively constant pupal mass over host tree families, but greater variation in development times.

This study is the first to measure the effect of food quality on the winter and scarce umber moth, in addition to the much studied autumnal moth. The results suggest a much stronger ability to adapt to genetic, environmental and geographical variation in

host plant quality in the winter moth than in the autumnal moth (Figures 1 and 2 and Table 2 in study **II**). The results for the scarce umber moth were similar to those for winter moth. Mountain birch quality affected the fecundities of all three species in the same direction. Thus no indirect effects on resident moth species are expected due to changes in host plant responses to defoliation inflicted by the invasive moth species. However, other organisms may be diversely affected by the birch response to moth defoliation; thus an increase in defoliator selection pressure may increase the exposure of mountain birches to other threats, such as pathogens (Ahlholm et al. 2002).

3.3 Direct and indirect competition

3.3.1 Direct competition

Evidence of asymmetric effects of direct competition via either behavioural interaction or exploitation competition was observed in study **III**. Living in close contact with the competing resident species did not significantly affect winter moth fecundity. The development time of winter moth larvae was likewise unaffected by the presence of autumnal moths. The survival probability of winter moths, however, was significantly higher when living together with autumnal moths than when living with conspecifics in single-species mesh bags (Figure 4 in study **III**).

In general density had a negative effect on both autumnal and winter moth larvae, as also observed in previous studies (Tammaru et al. 2000, Ruohomäki et al. 2003, Klemola et al. 2008). The fecundity of the autumnal moth, however, was affected by larval density already at lower levels compared to winter moth fecundity, which was significantly affected only at the highest larval densities. In addition, the fecundity of autumnal moth females was observed to be slightly lower already at low densities when winter moths were present in the same mesh bags compared to their fecundity in the single-species bags (Figure 2A in study **III**).

Overall, the results show that the resident autumnal moth may be more negatively affected by the presence of competing species than the invasive winter moth. This may be due to behavioural differences in feeding. Winter moth larvae tend to prefer feeding in mountain birch leaves loosely wound together with silk threads, while autumnal moths feed freely on the leaves (Tenow 1972 and pers. obs.). Autumnal moths may find leaves wound together by winter moths a less desirable food than free leaves.

As a consequence of these feeding behaviours, intraspecific competition may be more important for winter moth larvae than inter-specific direct competition. In a situation where the amount of leaves is restricted, winter moths may have better access to leaves when living with autumnal moths that browse from leaf to leaf than when living with conspecifics that occupy a leaf roll. The feeding behaviour of winter moths may be the reason behind the increased survival probability of the invader when living with the

resident autumnal moth in comparison to winter moths living in single-species mesh bags.

3.3.2 Indirect and apparent competition

Comparison of the performance of autumnal and winter moths feeding on the same tree as against single-species trees yielded slight indications of apparent competition via host plant (**III**). Moth performance was not directly affected by the presence of another species feeding on the same tree. Autumnal moth fecundity, on the other hand, diminished more radically with increasing defoliation of the mixed-treatment trees than in the single-treatment ones (Figure 1 in study **III**). While an overall negative effect of defoliation was predictable (e.g. Ruohomäki et al. 2003), the asymmetrical effect on the reproductive output of autumnal moths may reflect slight changes in the quality of mountain birch as food due to the invasive winter moth. Thus the results are evidence of indirect competition via the host plant, with a (more) negative effect on the resident autumnal moth.

Vertebrate and invertebrate generalist predators attacked winter moth pupae nearly three times more often than autumnal moth pupae, independent of pupal density (**IV** and **V**), although with some environmental variation (**V**). Despite the observed preference, the probability of predation did not differ between the mixed-treatment and the single-treatment (**V**). In addition, predators responded to both moth densities in an exponential asymptotic manner (Table 1 and Figure 2 in study **IV**). No evidence was thus found of short-term apparent competition between the resident and the invasive species via generalist predators.

In study **V**, autumnal and winter moths were found to share some of their larval parasitoids (Table 2 in study **V**). Larval parasitism rates were notably higher for autumnal than winter moths, showing a clear preference towards the resident species (Figure 3 in study **V**). However, no differences were observed between the mixed-treatment and single-species larval exposure treatment. There thus seems again to be no short-term apparent competition between autumnal and winter moths via specialist parasitoids.

The observed differences in pupal predation may account for the observed time lag in moth population dynamics, affecting the bottom and early increase phases of the cycles (e.g. Morris et al. 1958, Turchin 2003). The predation preference of invertebrate pupal predators towards winter moths could cause a later start of the increase phase for winter moth population cycles (**IV** and **V**). A comparison of the response curves (Figure 2 in study **IV**) also suggests that the predator community becomes saturated at much lower densities of autumnal than of winter moth pupae. As a consequence, autumnal moths are seemingly able to escape the regulating influence of their generalist natural enemies at much lower population densities than winter moths. This

could allow a more rapid population size increase for autumnal moths, with winter moth densities following with a lag, as observed in nature.

The parasitism preference for autumnal moths is another possible explanation for the divergent population dynamics of autumnal and winter moths (**V**). Parasitoids are nearly absent in the early increase phase of cycles in the mountain birch system, but parasitism rates increase rapidly at the peak and post-peak phases of the cycle at least for autumnal moths (Tenow 1972, Bylund 1995, Ruohomäki et al. 2000, Klemola et al. 2007). The asymmetric preference of parasitoids may cause an earlier collapse of the autumnal moth density but allow winter moths still increasing to their own peak density.

Application of the two-host–one parasitoid model, with the asymmetric effects of generalist predator and specialist parasitoid preferences, indeed successfully generated the observed divergent population dynamics (**VI**). With the parameters of observed equal realized fecundity, equal carrying capacity and mortality, differences in parasitoid preference, and the effects of asymmetric competition via generalist predators, the model was able to produce the observed asynchronous population cycles observed in Hana (Figure 1 in study **V**, Figures 5 and 6 in study **VI**). However, trait evolution in the modelled system seems to follow a branching-extinction cycle (Figure 3B in study **VI**). This implies that the observed asynchronous cycles may not persist over an evolutionary time scale, but that drastic changes in the community may be inflicted by the invasive moth species.

According to previous observations, when parasitoid preference towards two hosts is not equal, the effect of interactions is often positive for the less vulnerable species and negative for the more vulnerable one (Brassil & Abrams 2004). Indeed, our model showed that in most cases the average population density of the resident species, with higher parasitism rates, was reduced by the invasion of a closely related species (Figure 5 and Figure 4B in study **VI**). It has previously been reported that cyclic dynamics often dampen the effect of apparent competition (Abrams et al. 1998); the negative effect found here, however, was observed irrespective of the population dynamics in the modelled system (Figure 4B in study **VI**).

Alternatively to cycles that covered little over half of the dynamics observed in coexistence (Figure 4A in study **VI**), moth population densities in the model were able to reach quite stable dynamics (Figure 5). The dominant species, however, was not always defined by lower parasitoid preference: the species with a higher population density was not the same for all pairs of parasitism rates in the study (Figure 5). When differences in parasitism preference were pronounced, the modelled dynamics led in at least one case to the extinction of the preferred species (Figure 5).

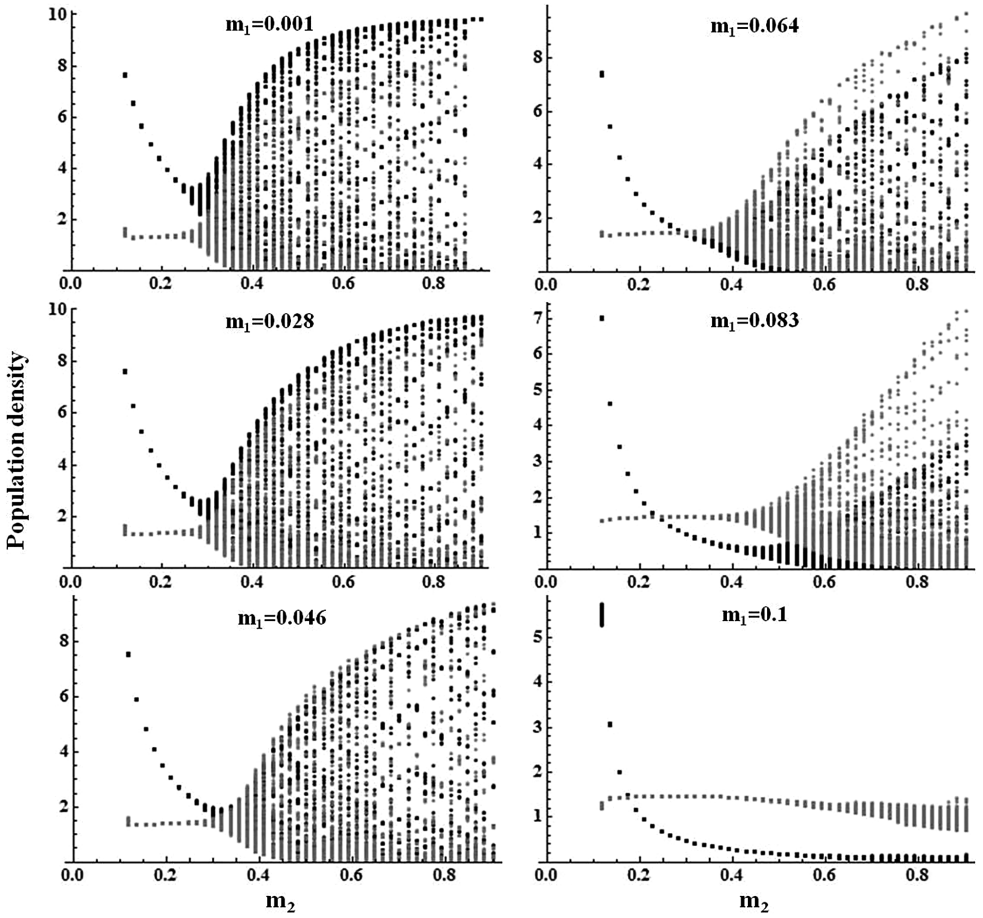

Figure 5. Possible population dynamics in the parameter area of coexistence. Population densities are shown for moth species 1 (gray) and 2 (black) for parameter pairs (m_1, m_2) in the parameter area, where coexistence is possible in the two-host– one parasitoid population dynamics. Parameter m_i describes the asymmetric effect of interspecific interactions for species *i*. More than half of the parameter space investigated produced cyclic dynamics. Where non-cyclic dynamics were observed, the outcome of the population densities varied according to the parameters. Moth species 1 represents an invader species with lower parameter values of m and moth species 2 a resident species with higher parameter values of m.

4. CONCLUSIONS

Over the last 60 years, the winters in northern Fennoscandia have become clearly milder (Figure S2 in study **I**). These milder winters have allowed winter moths to expand their range to new areas and to invade continental areas of Finnish Lapland (Jepsen et al. 2008, Klemola et al. 2008). The findings of this thesis suggest that in the future winter minimum temperatures will be even less important in determining the abundances of the invasive winter moth, as well as those of a potential invader, the scarce umber moth (**I**). Thus winter moths, and to a lesser extent scarce umber moths, can be expected to spread to much larger areas in the north than their current distribution. The range of possible changes in present interactions within the boreal and sub-arctic ecosystem may thus likewise change from a small local scale to larger regional one.

Winter moths have been found in continental Finnish Lapland for several years now (Klemola et al. 2008), and they interact with the mountain birch ecosystem directly on several trophic levels. Although herbivores can be greatly affected by the quality of their host plant, food quality affected the winter moth to a lesser extent than the resident autumnal moth (**II**). This is probably due to a higher adaptation capacity in the invasive species, and its ability to compensate (**II**). Clearly, the distribution of the winter moth population is not shaped by variation in mountain birch quality as a food for defoliators.

Direct or indirect competition with the resident autumnal moth is also unlikely to restrict the distribution of the invading winter moth. Quite the contrary: the winter moth seemed to be a better competitor, affecting autumnal moth fecundity especially at high densities and even benefitting from coexistence (**III**). Pupal predators, on the other hand, seemed to prefer winter moth pupae over those of the autumnal moth (**IV**). Nevertheless, as generalist predators are only likely to affect the species at low population densities (Turchin 2003, **IV**), the observed preference might not affect species abundance as a whole. On the other hand, specialist parasitoids are also able to respond to high population densities (Berryman et al. 1996, Klemola et al. 2010). Parasitism rates for the winter moth, however, were significantly lower than those for the autumnal moth (**V**).

While the two moth species shared some parasitoids in the new outbreak area as well, it is possible, that parasitoids specialised in winter moths had not yet been able to follow their host species to the new outbreak area, or that parasitoids in the new area are too imprinted on the resident autumnal moth to affect the winter moth population significantly. Furthermore, the study year represented a post-outbreak year for the autumnal moth but a peak year for the winter moth; thus the parasitism rates may have been naturally high for autumnal moths and low for winter moths. After study **V** was completed, in 2009-2010, a gregarious braconid parasitoid was found in a large

proportion of winter moth larvae (T. Klemola personal communication). It thus seems that after seven years a specialist parasitoid for the winter moth was able to follow its host range expansion. This delayed expansion of the specialist parasitoid indicates a delayed density-dependent response in parasitoids to winter moth population densities. It is thus possible, that parasitoids are behind the cycles of the winter moth as well as for those of the autumnal moth

The invasive winter moth was observed to have some indirect effects on the mountain birch ecosystem. Indirect apparent competition via the host plant affected the resident species, but had no negative effect on the invader. The findings presented in this thesis, however, show that the invader is not likely to affect the direction of selection pressure on the mountain birch (**II**), thus not inflicting any indirect effects on the resident species via the host plant in this manner.

Short-term apparent competition between the two species via generalist pupal predators or parasitoids was not observed. However, since direct interactions were observed especially in relation to higher density, any asymmetric factor influencing population densities is likely to induce additional indirect apparent effects. Predation on winter and autumnal moths can thus cause indirect asymmetric effects in this manner to lesser extent, since generalists can respond to moth densities only at low cycle phases. Parasitoids, however, can have more influence on moth abundances (Klemola et al. 2010) and are thus more likely to cause indirect effects.

The effects of apparent competition were indeed observed on a longer time scale with the mathematical model (**VI**). The results of the modelled dynamics suggest that long-term apparent competition, with a negative impact on the resident species, occurs in a major portion of the parameter area. In addition, generalist predators and parasitoids might produce the asynchronous population dynamics observed. However, the lack of a stable attractor in the modelled system implies that the asynchronous cycles observed at the beginning of the invasion may not persist over an evolutionary time frame. Alternative population dynamics included cycles with different amplitudes, stable population densities with the winter moth and autumnal moth alternating as the dominant species, and the extinction of the resident defoliator.

Many of the interactions between the invaders and the mountain birch community were investigated in this thesis for the first time. Little effort has likewise been made previously in modelling this seemingly simple, yet actually highly complex ecosystem. These studies have shown that the interactions between the invaders and the local ecosystem are affected by a multitude of factors. However, few restrictive effects, or none, were observed for the invasive winter moth. On the contrary: the invader actually had negative impact on the resident species, through direct and indirect interactions. The long cycles of both of these defoliator species limits the extent to which the overall impact of the invader can be seen in the mountain birch ecosystem over a short time

scale. In addition, the invasion of the winter moth is a relatively new phenomenon; thus the interactions may still change, due for example to new parasitoid species tracking the expansion of the winter moth's range. Nevertheless, the modelling of long-term interactions between the resident autumnal moth and the invasive winter moth with their currently shared enemies showed that drastic changes in the northern ecosystem may be taking place. Possible future scenarios include the persistence of three-species cycles with high and long-lasting defoliation pressure on the mountain birch, or alternatively the extinction or radical reduction of the resident species. To conclude: winter moths may be able to further expand their species range to more continental areas; they may thereby inflict direct and indirect effects on the resident autumnal moth and the whole mountain birch community, over both a small and a large geographical area, and over both a short-term and a long-term time scale.

5. ACKNOWLEDGEMENTS

During my PhD work, I had the fortune of having three supervisors. Tero and Kari first suggested this topic to me, and Kalle was willing to supervise the mathematical modelling, which I wanted to include in my thesis. In my opinion, more cooks made a better soup in this case. Through the different backgrounds and views of my supervisors, I was able to see my work from many perspectives. I also gained from all of their individual knowledge and from the fruitful conversations we had. In addition, I was able to learn a lot about the life as a scientist from all of my supervisors, a skill that I will certainly benefit from in the future. I owe special gratitude to Tero, who has been my supervisor already during my MSc work and has an amazing patience listening to my frantic talking about new ideas, the sometimes over-enthusiastic explanations about the results and the almost never-ending questions on statistics. Thank you for listening and discussing during all these years! Thank you, Kari, for sharing your knowledge about the genetic side of ecology and for pushing me to think my work in a larger scale and in the context of plants. And thank you, Kalle, without whom many complexities in the mathematical modelling would have remained unsolved and interesting results would have remained unreported.

Of course, without the background work of everyone in the autumnal moth and mountain birch projects during the years this work would not have been possible to accomplish. Special thanks to Kai Ruohomäki, who is a dedicated autumnal moth guru, and answered many of my little and big questions during these years. I thank also Tommi for being a great colleague and for sharing his seemingly unlimited knowledge.

Without the contribution of my co-authors the work would not have been the same. Netta, even if you might not know it, you have found the right thing to say in several occasions and helped me in and outside the field. Annette, thank you for the time you were with us in Finland, you brought a lot of new perspective to the work. I also thank Timo Kaukoranta and Tapani Repo for adding new elements to my work and helping with new methods.

The hard work of all the assistants in the field is highly appreciated. Sorry for the physically demanding and never-ending “bag rounds” and “bucket larvae” and thank you: Salla Härkönen, Aino Kalske, Saara Koutaniemi, Kukka Kyrö, Juho Lämsä, Elisa Männistö, Aija Nieminen, Kati Pihlaja, Elina Salo, Hanna Urtti and Ilona Välimaa.

I would also like to thank the staff at Kevo Subarctic Research Institute for the facilities and help. Special thanks to Lasse Iso-Iivari for providing information and Aarne Sujala for saving me from a cold ride to Nuorgam on a scooter. The articles and manuscripts were checked for language by Kevin O’Brien and John Stotesbury. The language of the thesis was kindly checked by Ellen Valle. I’m also grateful for all the comments and discussions I have had with the PhD students at the Section of Ecology

and at the Biology Department overall. Thank you also Liisa, for the discussions and comments we have shared along with the office.

I thank my friends, Hanna-Mari, Jaana, Maija, Martiina and Satu, from the bottom of my heart. Thank you all for sharing the journey through the studies at the university and sharing the life outside the university as well. I thank also Mika, from my heart, for supporting me. Last but definitely not least, I thank my family: mom Ulla, dad Ray and my sister Ina. Thank you all for listening, supporting, encouraging and enjoying with me, even though you might not have always known exactly what I am talking about.

This work has been financially supported by Maj and Tor Nessling Foundation, Turku University Foundation and Academy of Finland (projects to Tero Klemola and Kalle Parvinen).

6. REFERENCES

Abrams P.A., Holt R.D. & Roth J.D. 1998: Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* 79:201–212.

Ahlholm J. Helander M., Elamo P., Saloniemi I., Neuvonen S., Hanhimäki S. & Saikkonen K. 2002: Micro-fungi and invertebrate herbivores on birch trees: fungal mediated plant-herbivore interactions or response to host quality? *Ecology Letters* 5:648–655.

Anderson K.E., Inouye B.D. & Underwood N. 2009: Modeling herbivore competition mediated by inducible changes in plant quality. *Oikos* 118:1633–1646.

Ayres M.P. & MacLean Jr. S.F. 1987: Development of birch leaves and the growth energetic of *Epirrita autumnata* (Geometridae). *Ecology* 68:558–568.

Bale J.S. 1991: Insects at low temperature: a predictable relationship? *Functional Ecology* 5:291–298.

Bale J.S., Masters G.J., Hodkinson I.D., Awmack C., Bezemer T.M., Brown V.K., Butterfield J., Buse A., Coulson J.C., Farrar J., Good J.G., Harrington R., Hartley S., Jones T.H., Lindroth R.L., Press M.C., Symrnioudis I., Watt A.D. & Whittaker J.B. 2002: Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.

Bale J.S. & Hayward S.A.L. 2010: Insects overwintering in a changing climate. *The Journal of Experimental Biology* 213:980–994.

Berggren Å., Björkman C., Bylund H. & Ayres P. 2009: The distribution and abundance of animal populations in a climate of uncertainty. *Oikos* 118:1121–1126.

Berryman A.A. 1996: What causes population cycles of forest Lepidoptera? *Trends in Ecology and Evolution* 11:28–32.

Brassil C.E. & Abrams P.A. 2004: The prevalence of asymmetrical indirect effects in two-host–one-parasitoid systems. *Theoretical Population Biology* 66:71–82.

Bylund H. 1995: Long-term interactions between the autumnal moth and mountain birch: the roles of resources, competitors, natural enemies, and weather. Ph.D. thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Bylund H. 1999: Climate and the population dynamics of two insect outbreak species in the north. *Ecological Bulletins* 47:54–62.

Chase J.M., Abrams P.A., Grover J.P., Diehl S., Chesson P., Holt R.D., Richards S.A., Nisbet R.M. & Case T.J. 2002: The interaction between preadation and competition: a review and synthesis. *Ecology Letters* 5:302–315.

Chesson P. 2000: Mechanisms of maintenance of species diversity. *Annual Review Ecology and Systematics* 31:343–366.

Colautti R.I. & MacIsaac H.J. 2004: A neutral terminology to define 'invasive' species. *Diversity and Distributions* 10:135–141.

Connell J.H. 1961: The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.

Connell J.H. 1983: On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122: 661–696.

Delatte H., Duyck P-F., Triboire A., David P., Becker N., Bonato O. & Reynaud B. 2009: Differential invasion success among biotypes: case of *Bemisia tabaci*. *Biological Invasions* 11:1059–1070.

DeMoraes C.M., Lewis W.J., Paré P.W., Alborn H.T. & Tumlinson J.H. 1998: *Nature* 393:570–573.

Denno R.F., McClure M.S. & Ott J.R. 1995: Interspecific interactions in phytophagous insects: competition re-examined and resurrected. *Annual Review of Entomology* 40:297–331.

Denno R.F., Peterson M.A., Gratton C., Cheng J.A., Langellotto G.A., Huberty A.F. & Finke D. 2000: Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* 81:1814–1827.

Denno R.F., Lewis D. & Gratton C. 2005: Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici* 42:295–311.

Falconer D.S. & Mackay T.F.C. 1996: *Introduction to quantitative genetics*. 4th edn, Longman Group Ltd, Harlow, UK.

Fry J.D. 2004: Estimation of genetic variances and covariances by Restricted Maximum Likelihood using PROC MIXED. In Saxton, A., ed. *Genetic analysis of complex traits using SAS*. Cary, NC: SAS Institute Inc.

Gaston K.J., Genney D.R., Thurlow M. & Hartley S.E. 2004: The geographical range structure of the holly leaf-miner. IV: Effects of variation in host-plant quality. *Journal of Animal Ecology* 73:911–924.

Hagen S.B., Jepsen J.U., Ims R.A. & Yoccoz N.G. 2007: Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography* 30:299–307.

Hairston et al. N.G., Smith F.E. & Slobodkin L.B. 1960: Community structure, population control and competition. *The American Naturalist* 44:421–424.

Hanhimäki S., Senn J. & Haukioja E. 1994: Performance of insect herbivores on hybridizing trees: the case of the subarctic birches. *Journal of Animal Ecology* 63:163–175.

Harrison S. & Karban R. 1986: Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. *Oecologia* 69:354–359.

Haukioja E. 2005: Plant defences and population fluctuations of forest defoliators: mechanism-based scenarios. *Annales Zoologici Fennici* 42:313–325.

Haukioja E. & Neuvonen S. 1985: The relationship between size and reproductive potential in male and female *Epirrita autumnata* (Lep., Geometridae). *Ecological Entomology* 10:267–270.

Haukioja E., Neuvonen S., Hanhimäki S. & Niemelä P. 1988: The autumnal moth in Fennoscandia. In A.A. Berryman (ed.): *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*, pp. 163–178. Plenum, New York.

Heisswolf A., Klemola T., Andersson T. & Ruohomäki K. 2009: Shifting body weight-fecundity relationship in a capital breeder: maternal effects on egg numbers of the autumnal moth under field conditions. *Bulletin of Entomological Research* 99:73–81.

Hickling R., Roy D.B., Hill J.K., Fox R. & Thomas C.D. 2006: The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12:450–455.

Hogstad O. 2005: Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: a 30-year study. *The Ibis* 147:77–91.

Holt R.D. 1977: Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.

Holt R.D. 2009: Up against the edge: invasive species as testbeds for basic questions about evolution in heterogeneous environments. *Molecular Ecology* 18:4347–4348.

Holt R.D. & Lawton J.H. 1993: Apparent competition and enemy-free space in insect host-parasitoid communities. *The American Naturalist* 142:623–645.

Holt R.D. & Lawton J.H. 1994: The ecological consequences of natural enemies. *Annual Review of Ecology and Systematics* 25:495–520.

Horner J.D. & Abrahamson W.G. 1992: Influence of plant genotype and environment on oviposition preference and offspring survival in gallmaking herbivore. *Oecologia* 90:323–332.

Houle D. 1992: Comparing evolvability and variability of quantitative traits. *Genetics* 130:195–204

Jepsen J.U., Hagen S.B., Ims R.A. & Yoccoz N.G. 2008: Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology* 77:257–264.

Jepsen J.U., Hagen S.B., Karlsen S-R. & Ims R.A. 2009: Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. *Proceedings of the Royal Society of London, Series B* 276:4119–4128.

Jepsen J.U., Kapari L., Hagen S.B., Schott T., Vindstad O.P.L., Nilssen A.C. & Ims R.A. 2011: Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. *Global Change Biology* in press.

Jones C.G., Ostfeld R.S., Richard M.P., Schrauber E.M. & Wolff J.O. 1998: Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279:1023–1026.

Kallio P., Hurme H., Eurola S., Norokorpi Y. & Sepponen P. 1986: Research activities on the forest line in Northern Finland. *Arctic* 39:52–58.

Kaplan I. & Denno R.F. 2007: Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecology Letters* 10:977–994.

Kenis M., Auger-Rozenburg M-A., Roques A.,Timms L., Péré C., Cock M.J.W, Settele J., Augustin S. & Lopez-Vaamonde C. 2009: Ecological effects of invasive alien insects. *Biological Invasions* 11:21–45.

Klemola N., Andersson T., Ruohomäki K. & Klemola T. 2010: Experimental test of parasitism hypothesis for population cycles of a forest lepidopteran. *Ecology* 91:2506–2513.

Klemola T., Tanhuanpää M., Korpimäki E. & Ruohomäki K. 2002: Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99:83–94.

Klemola T., Klemola N., Andersson T. & Ruohomäki K. 2007: Does immune function influence population fluctuations and level of parasitism in the cyclic geometrid moth? *Population Ecology* 49:156–178.

Klemola T., Andersson T. & Ruohomäki K. 2008: Fecundity of the autumnal moth depends on pooled geometrid abundance without a time lag: implications for cyclic population dynamics. *Journal of Animal Ecology* 77:597–604.

Kolar C.S. & Lodge D.M. 2001: Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16:199–204.

Lambrinos J.G. 2004: How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology* 85:2061–2070.

Lau J.A. 2008: Beyond the ecological: biological invasions alter natural selection on native plant species. *Ecology* 89:1023–1031.

Lee C.E. 2002: Evolutionary genetics of invasive species. *Trends in Ecology & Evolution* 17:386–391.

Lehtonen J. 1987: Recovery and development of birch forests damaged by *Epirrita autumnata* in Utsjoki area, North Finland. *Reports of the Kevo Subarctic Research Station* 20:35–39.

Lehtonen J. & Heikkinen R.K. 1995: On the recovery of mountain birch after *Epirrita* damage in Finnish Lapland, with a particular emphasis on reindeer grazing. *Ecoscience* 2:349–356.

Lindner M., Garcia-Gonzalo J., Kolström M., Green T., Reguera R., Maroschek M., Seidl R., Lexer M.J., Netherer S., Schopf A., Kremer A, Delzon S., Barbati A., Marchetti M. & Corona P. 2008: Impacts of climate change on European forests and options for adaptation. *Report to the European Commission Directorate-General for Agriculture and Rural Development*, November 2008.

Lockwood J.L., Hoopes M., Marchetti M.P. 2007: *Invasion ecology*, 312 pp., Blackwell Publishing, Oxford, UK.

Lodge D.M. 1993: Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* 8:133–137.

Luoto M., Heikkinen R.K., Pöyry J. & Saarinen K. 2006: Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* 33:1764–1778.

MacArthur R.H. 1958: Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599–619.

MacPhee A.W. 1967: The winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), a new pest in Nova Scotia, and its coldhardiness. *Canadian Entomologist* 99:829–834.

McGeoch M.A. & Price P.W. 2004: Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology* 73:506–516.

McLaughlin J.F., Hellman J.J., Boggs C.L. & Ehrlich P.R. 2002: Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences* 99:6070–6074.

Menéndez R., González-Megías A., Lewis O.T., Shaw M.R. & Thomas C.D. 2008: Escape from natural enemies during climate-driven range expansion: a case study. *Ecological Entomology* 33:413–421

Mjaaseth R.R., Hagen S.B., Yoccoz N.G. & Ims R.A. 2005: Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore–mountain birch system. *Oecologia* 145:53–65.

Mooney H.A. & Cleland E.E. 2001: The evolutionary impact of invasive species. *Proceedings of the National Academy of Science* 98:5446–5451.

Morris R.F., Cheshire W.F., Miller C.A. & Mott D.G. 1958: The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* 39:487–494.

Morris R.J., Lewis O.J. & Godfray H.C.J. 2005: Apparent competition and insect community structure: towards a spatial perspective. *Annales Zoologici Fennici* 42:449–462.

Murdoch W.W. 1966: "Community structure, population control and competition" – a critique. *The American Naturalist* 100:219–226.

Nilssen A.C. 2007: En ny art lauvmakk har kommet til Nord-Norge. *Ottar* 268:27–31.

Nilssen A. & Tenow O. 1990: Diapause, embryo growth and supercooling capacity of *Epirrita autumnata* eggs from northern Fennoscandia. *Entomologica Experimentalis et Applicata* 57:39–55.

Parmesan C. 2006: Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37:637–669.

Parmesan C., Ryrholm N., Stefanescu C., Hill J.K., Thomas C.D., Descimon H., Huntley B., Kaila L., Kullberg J., Tammaru T., Tennent W.J., Thomas J.A. & Warren M. 1999: Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.

Preisser E.L. & Elkington J.S. 2008: Exploitative competition between invasive herbivores benefits a native host plant. *Ecology* 89:2671–2677.

Price P.W., Bouton C.E., Gross P., McPheron B.A., Thompson J.N. & Weis A.E. 1980: Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11:41–65.

Redman A.M. & Scriber J.M. 2000: Competition between the gypsy moth, *Lymatria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia* 125:218–228.

Roslin T. Gripenberg S., Salminen J-P., Karonen M., O'Hara R.B., Pihlaja K. & Pulkkinen P. 2006: Seeing the trees for the leaves – oaks as mosaics for a host-specific moth. *Oikos* 113:106–120.

Roslin T. & Salminen J-P. 2009: A tree in the jaws of a moth – temporal variation in oak leaf quality and leaf-chewer performance. *Oikos* 118:1212–1218.

Ruohomäki K., Tanhuanpää M., Ayres M.P., Kaitaniemi P., Tammaru T. & Haukioja E. 2000: Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Population Ecology* 42:211–223.

Ruohomäki K., Klemola T., Kaitaniemi P. & Käär M. 2003: Crowding-induced responses in a geometrid moth revisited: a field experiment. *Oikos* 103:489–496.

Sakai A.K., Allendorf F.W., Holt J.D., Lodge D.M., Molofsky J., With K.A., Baughman S., Cabin R.J., Cohen J.E., Ellstrand N.C., McCauley D.E., O'Neil P., Parker I.M., Thompson J.N. & Weller S.G. 2001: The population biology of invasive species. *Annual Review of Ecology and Systematics* 32:305–332.

Schädler M., Brandl R. & Kempel A. 2010: Host plant genotype determines bottom-up effects in an aphid-parasitoid-predator system. *Entomologia Experimentalis et Applicata* 135:162–169.

Schoener T.W. 1974: Resource partitioning in ecological communities. *Science* 185:27–39.

Smith S.A. & Beaulieu J.M. 2009: Life history influences rates of climatic niche evolution in flowering plants. *Proceedings of the Royal Society of London, Series B* 276:4345–4352.

Stevens M.T., Waller D.M. & Lindroth R.L. 2007: Resistance and tolerance in *Populus tremuloides*: genetic variation, costs, and environmental dependency. *Evolutionary Ecology* 21:829–847.

Strauss S.Y. & Irwin R.E. 2004: Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annual Review of Ecology, Evolution and Systematics* 35:435–466.

Strauss S.Y., Lau J.A. & Carroll S.P. 2006: Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters* 9:357–374.

Suomela J. & Ayres M.P. 1994: Within-tree and among-tree variation in leaf characteristics of mountain birch and its implications for herbivory. *Oikos* 70:212–222.

Suomela J. & Nilson A. 1994: Within-tree and among-tree variation in growth of *Epirrita autumnata* on mountain birch leaves. *Ecological Entomology* 19:45–56.

Tammaru T., Kaitaniemi P. & Ruohomäki K. 1996: Realized fecundity in *Epirrita autumnata* (Lepidoptera: Geometridae): relation to body size and consequences to population dynamics. *Oikos* 77:407–416.

Tammaru T., Ruohomäki K. & Montola M. 2000: Crowdinginduced plasticity in *Epirrita autumnata* (Lepidoptera: Geometridae): weak evidence of specific modifications in reaction norms. *Oikos* 90:171–181.

Tanhuanpää M., Ruohomäki K., Kaitaniemi P. & Klemola T. 1999: Different impact of pupal predation on populations of *Epirrita autumnata* (Lepidoptera; Geometridae) within and outside the outbreak range. *The Journal of Animal Ecology* 68:562–570.

Tenow O. 1972: The outbreaks of *Oporinia autumnata* Bkh. & *Operophthera* spp. (Lep., Geometridae) in the Scandinavianmountain chain and northern Finland 1862–1968. *Zoologiska Bidrad fr°an Uppsala, Supplement* 2:1–107.

Tenow O. 1996: Hazards to a mountain birch forest—Abisko in perspective. *Ecological Bulletins* 45:104–114.

Tenow O., Nilssen A.C., Bylund H. & Hogstad O. 2007: Waves and synchrony in *Epirrita autumnata*/*Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. *Journal of Animal Ecology* 76:258–268.

Tsutsui N.D., Suarez A.V., Holway D.A. & Case T.J. 2000: Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Science* 97:5948–5953.

Turchin P. 2003: Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press.

Turnock W.J. & Fields P.G. 2005: Winter climates and coldhardiness in terrestrial insects. *European Journal of Entomology* 102:561–576.

Tylianakis J.M., Didham R.K., Bascompte J. & Wardle D.A. 2008: Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11:1351–1363.

Underwood N. 2009: Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect. *Journal of Animal Ecology* 78:839–847.

van Veen F.J.F., Morris R.J. & Godfray H.C.J. 2006: Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51:187–208.

Veteli T.O., Repo T., Niemelä P. & Varama M. 2005: Geographic variation in winter freezing susceptibility in the eggs of the European pine sawfly (*Neodiprion sertifer*). *Agricultural and Forest Entomology* 7:115–120.

Virtanen T., Neuvonen S. & Nikula R. 1998: Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera: Geometridae) with a Geographical Information system: predictions for current climate and warmer climate scenarios. *Journal of Applied Ecology* 35:311–322.

Virtanen T. & Neuvonen S. 1999: Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia* 120:92–101.

Walther G-R., Roques A., Hulme P.E., Sykes M.T., Pyšek P., Kühn I., Zobel M., Bacher S. Botta-Dukát Z., Bugmann H., Czúcz B., Dauber J., Hickler T., Jarošik V., Kenis M., Klotz S., Minchin D., Moora M., Nentwig W., Ott J., Panov V.E., Reineking B., Robinet C., Semenchenko V., Solarz W., Thuiller W., Vilà M., Vohland K. & Settele J. 2009: Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* 24:686–693.

Wielgolaski F.E. 1972: Vegetation types and plant biomass in tundra. *Arctic and Alpine Research* 4:291–305.

Wise M.J. 2009: Competition among herbivores of *Solanum carolinense* as a constraint on the evolution of host-plant resistance. *Evolutionary Ecology* 23:347–361.